Estimates of Larval-Fish Abundance: Diurnal Variation and Influences of Sampling Gear and Towing Speed¹

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Abstract

The influence of net-towing speed on estimates of the abundance of larval Atlantic menhaden Brevoortia tyrannus, spot Leiostomus xanthurus, pinfish Lagodon rhomboides, and Atlantic croaker Micropogonias undulatus was studied in nearshore and estuarine areas of North Carolina. A modified Miller high-speed sampler was towed at speeds ranging from 2 to 12 m/second. In one series, catch increased monotonically with increasing tow speed up to 7 m/second; in a second series, catch increased with speed up to 8 m/second but decreased at higher speeds, possibly because larvae were extruded through the net or deflected by the pressure wave. In additional studies, a slowly towed (2 m/second) 20-cm bongo net was compared to the high-speed sampler during daylight; day and night samples from the high-speed sampler also were compared. These data imply that visual avoidance by larval fish biases estimates of both their abundance and their vertical distribution. The data from all three studies suggest the need to calibrate nets for towing-velocity effects, particularly for larger ichthyoplankton (10–16-mm spots and 19–26-mm Atlantic menhaden) that can avoid slowly towed sampling gear more easily than can earlier life stages.

Gears used to sample ichthyoplankton quantitatively usually are towed at speeds from 0.5 to 2 m/second. A major assumption behind any quantitative plankton-sampling program is that the sample accurately represents the assemblages and abundances of species in the water column through which the sampler is towed. Although there are inconsistencies in published data, numerous investigators have pointed out that avoidance of nets by late-stage larval and juvenile fishes occurs, and that such avoidance increases at lower tow speeds (Miller 1961; Barkley 1964; Smith et al. 1964; Clutter and Anraku 1968; Colton et al. 1980). Barklev's (1972) theoretical analysis of the capture probability for fish in towed samplers implies an asymptotic relation between catch and tow speed.

The causes of variable catches of larval fish, as they relate to sampler size and speed, have

been considered by several authors (see Barkley 1964; Clutter and Anraku 1968; Aron and Collard 1969: Schnack 1974: Bowles and Merriner 1978). Quirk, Lawler, and Matusky Engineers (cited in Bowles and Merriner 1978), for example, reported that large-mouth nets caught more larvae of white perch Morone americana at lower speeds, but smaller-mouth nets were more efficient at higher tow speeds. In part, net avoidance depends upon the size of the netmouth opening, the presence of pressure waves, the speed at which the gear is towed, and the distance at which the sampler is perceived by a larva. Colton et al. (1980) were unable to demonstrate differential avoidance by herring larvae (presumably, Atlantic herring Clupea h. harengus) smaller than 21 mm at tow speeds of 1.8 and 0.8 m/second but did indicate larger herring larvae would avoid nets towed at slow speeds. Because net avoidance is both size- and species-related, estimates of population size, species diversity, and vertical distribution of larval fish within the water column may be biased due to this factor. These problems are compounded by diurnal migrations and patchy distributions of organisms (Noble 1970). Night catches often exceed daylight catches, suggesting visual avoidance of sampling gear (Silliman 1943; Ahlstrom 1954, 1959; Arthur 1956;

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Bridger 1956) or changes in diurnal distribu-

The purposes of this paper are to present data on the influence of tow speed on estimates of larval-fish abundance obtained from a modified Miller high-speed sampler (Miller 1961), and to compare estimates of nearshore larval fish (>10 mm long) densities from a Miller highspeed sampler and a 20-cm bongo net. We hypothesized that if tow speed does influence catch of larvae, the relationship either would be asymptotic, or it would be parabolic if larvae are extruded through the net mesh or if they passively avoid the net because of the pressure wave at high velocities. If the relation were asymptotic, estimates of true density of larval fish would require that the asymptote of the density-velocity function be calculated, such as suggested by Barkley (1972). If the relationship were parabolic, the maximum of the parabola should provide a more accurate estimate of true density.

Methods

Speed trials were carried out in the nearshore zone near Beaufort Inlet (34°43'N, 76°42'W) and in the Intracoastal Waterway near the mouth of the Cape Fear River at Southport, North Carolina (34°0'N, 78°0'W). The highspeed sampler we used is a modification of the device described by Miller (1961). The sampler body is a 61-cm-long opaque, dark-green, fiberglass tube with an internal diameter of 14 cm. A 3.3-m net was used, the first 2.3 m of which was untapered and made of 947-μm mesh; the last 1.0 m was tapered and made of 252-μm mesh. We used a collection bucket made of polyvinyl chloride having a 252-μm nylonmesh window. Both the ratio of the net length to the mouth opening and large mesh of the anterior net insure good filtration and reduce the potentials for backwash and development of a pressure wave. Smith et al. (1968) indicated that if the open area of a net is more than 3.2 times that of the mouth, the filtration efficiency should be above 85%. Miller (1961) noted that at speeds of 2.5 to 5 m/second, there was no difference in total water flow through 1,024- μ m, 569- μ m, and 282- μ m nylon nets with his original design.

The sampler was towed either on a stationary frame from a small boat (estuarine samples) or, with a 23-kg depressor, from a cable suspended

on a winch from a larger vessel (nearshore samples). The most satisfactory supporting frame we have developed was made of 5-cm (outside diameter) stainless-steel pipe affixed to a mast on the boat. The leading edge of the pipe to which the sampler was attached had a wedgeshaped piece of wood affixed to act as a cutting edge and reduce resistance. The volume of water filtered was based on readings from a General Oceanics4 digital flowmeter that was attached to the outside of the fiberglass sampler body and calibrated over the entire speed range. No discernible difference in volume flow was observed between a meter mounted on the inside of the net mouth and one mounted on the outside of the sampler body at any tow velocity. When towed from a small boat, the sampler was outside the bow wave, 1.6 m from the side and 4.8 m from the intersection of the bow and water. All samples were taken from the side of the boat.

Tow-Speed Comparisons⁵

Speed trials were carried out in surface water (at a depth of 0.5 m) at 2, 4, 6, and 7 m/second approximately 0.8 km from shore between Cape Lookout and Beaufort Inlet, North Carolina, in 1977, and at 2, 4, 6, 8, 10, and 12 m/second in the Intracoastal Waterway (ICWW) near the Cape Fear River in 1978; we discontinued tows at 2 m/second in the ICWW after several runs because larval fishes were rare in the samples. Tow speeds were calibrated over timed distances and by use of engine revolutions. A randomized-block design was employed to determine the sequence of tows; each tow covered 1,850 m. Each complete series of tow speeds was a block in the design. Fourteen tow series (blocks) made up of 56 tows were carried out in 1977 and seven tow series of 35 tows were carried out in 1978; in each case approximately 60-70 m3 of water were filtered. All series in both years were run in March. All catches per volume (x) were transformed $(\log_{10}[x+1])$ to

⁴ Mention of trade names does not imply endorsement by the National Marine Fisheries Service.

⁵ Speeds used in various field trials were 4, 8, 10, 12, 14, 16, 20, and 24 knots. The rounded metric conversions used in this paper (2, 4, 5, 6, 7, 8, 10, and 12 m/second) are about 5% below nominal speeds. Analyses are not affected by this.

Table 1.—Average total catch (±SE) of fish larvae per 1,000 m³ during towing-speed trials with a Miller high-speed sampler, March 1977 and 1978, North Carolina.

Towing speed (m/second)	Beaufort Inlet (14 tows per speed)	Cape Fear River (7 tows per speed)
2	109 ± 53	
4	141 ± 47	16 ± 11
6	211 ± 70	52 ± 10
7	285 ± 94	
8		62 ± 25
10		53 ± 22
12		22 ± 14

normalize the data and were analyzed by analysis of variance. This transformation met the additivity assumption implicit in a randomized-block design (Box et al. 1978).

Sufficient numbers of Atlantic menhaden Brevoortia tyrannus, spot Leiostomus xanthurus, and pinfish Lagodon rhomboides were collected in the ocean samples near Beaufort to allow separate analyses of catch data for these species. For these analyses we used only data from complete series of tow speeds in which larvae were caught in at least 50% of the tows. Those blocks in which fish were caught only at one speed generally provided a density estimate of less than 10 larvae/1,000 m³ at that speed. Analysis of data for the speed trials in the ICWW was based on larvae of all species combined because we were unable to identify confidently those damaged larvae that were collected at tow speeds in excess of 8 m/second.

Gear and Day-Night Comparisons

We compared catch per volume for a bridleless 20-cm bongo net (333-µm mesh) towed at 2 m/second with catch per volume for a modified bridleless Miller high-speed sampler towed at 5 m/second. Tow speeds for 60-cm bongo nets in a standard MARMAP (Marine Resources Monitoring, Assessment, and Prediction) survey are recommended at 0.8 m/second (Powles and Stender 1976). We sampled at 2 m/second to increase the efficiency of the smaller 20-cm bongo because Quirk, Lawler, and Matusky Engineers (cited by Bowles and Merriner 1978) reported increased efficiency of small-mouth nets at higher tow speeds relative to large-mouth ones.

Table 2.—Analyses of variance of catch per unit volume for Atlantic menhaden and spots collected in a Miller high-speed sampler near Beaufort Inlet. Raw data were transformed: $\mathbf{x} = \log_{10}(\mathbf{x} + 1)$; asterisk (*) denotes P < 0.05.

	Atlar	ntic menhaden	Spot		
Source	df	Mean square	df	Mean square	
Blocks	13	3.9866	5	7.6704	
Velocity					
Linear	1	16.5055*	1	9.0027*	
Quadratic	1	4.3267	1	3.0775	
Cubic	1	4.6662	1	6.0001	
Error	39	2.4530	15	1.9311	
Nonadditivity	1	1.0620 NS	1	0.4651 NS	
Remainder	38	2.4869	14	2.0358	

Ten samples were collected in March 1977 with each net towed at each of two depths: surface (0.5 m) and near bottom (5–10 m) in the Beaufort Inlet and between the Inlet and Cape Lookout (40 tows, total). A bathykimograph was attached near the top of the samplers to estimate when they were close to the bottom. We hypothesized that if vision is important in avoidance, the ratio of the density estimates from the two gears would be greater at the surface, where illumination is greater.

In addition, 10 surface (0.5 m) and 10 bottom (5–10 m) tows with the Miller sampler were made both during the day and at night (40 samples in all) in the nearshore zone at Beaufort in March 1977. Towing speeds were 5 m/second. A surface tow was followed as soon as possible by a bottom tow.

Results and Discussion

Tow-Speed Comparisons

Tows near Beaufort Inlet were in clear coastal water, whereas those in the Intracoastal Waterway were in more turbid water. In both areas, there was a high degree of variability in the catch data (Table 1). The same species were collected in both areas. Atlantic menhaden dominated the catch; the majority of the remainder was spot, pinfish, and Atlantic croaker *Micropogonias undulatus*. Size ranges for the species were similar for both areas: 19–26 mm for Atlantic menhaden and 10–16 mm for pinfish, spot, and Atlantic croaker. Average larval-fish density was higher (187 larvae/1,000 m³) in

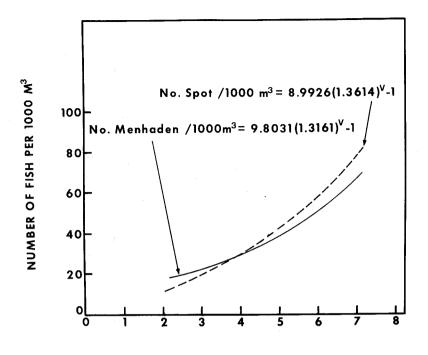


FIGURE 1.—Least squares regression lines for speed-trial data on Atlantic menhaden and spot collected near Beaufort Inlet. The exponent V is velocity.

VELOCITY IN METERS PER SECOND

the ocean area near Beaufort than in the ICWW (41 larvae/1,000 m³) near the Cape Fear River, although these differences may be temporal because samples were taken in different years.

Near Beaufort, there were significant increases (P < 0.05) in the catch of Atlantic menhaden and spots with increasing tow speed between 2 and 7 m/second (Table 2). Apparent densities of pinfish were relatively low at all tow speeds, decreased at 6 m/second, and increased at 7 m/second.

Least-squares regressions were used to test the relationship between estimated densities of Atlantic menhaden and spot and tow speed (Fig. 1). There was an approximate 5-fold increase in the estimate of respective geometric mean densities as the velocity of the sampler was increased from 2 to 7 m/second. The regression lines were not significantly different from one another and indicate that 10–16-mm spots and 19–26-mm Atlantic menhaden possess similar capabilities for avoiding the Miller sampler. Variations in abundance of larvae at the differ-

ent times that blocks of trials were made impart considerable variance around the regressions; correlation coefficients were 0.33 for spot and 0.31 for Atlantic menhaden.

Analysis of variance for the ICWW data indicated that there was a relationship between the logarithm of total catch and velocity (F = 3.0906; df = 4,24; P < 0.05), and that it was curvilinear (parabolic) (F = 11.46; df = 1,24; P < 0.0025) (Table 3). Ten of the 35 tows in the ICWW had zero catches of larvae; these were clustered at 4 and 12 m/second. We believe the lower densities measured at velocities greater than 7 m/second were due to extrusion or to pressure-wave-related passive avoidance.

The data for the speed trials in nearshore water and in the ICWW both are consistent with the hypothesis that as towing velocity is increased from 2 to 7 or 8 m/second, catch per unit volume monotonically increases. A curvilinear relation was defined for two species, Atlantic menhaden and spot. Further increase in tow velocity may result in a reduced catch as a

Table 3.—Analysis of variance of catch per unit volume for samples collected in the Intracoastal Waterway near the Cape Fear River, with a Miller high-speed sampler. Raw data were transformed: $x = \log_{10}(x+1)$; asterisk (*) denotes P < 0.01.

Source	df	Mean square
Block	6	2.9010
Velocity		
Linear	1	0.0924
Quadratic	1 -	31.5718*
Cubic	1	0.0343
Quartic	1	2.3654
Error	24	2.7537
Nonadditivity	1	1.9090 NS
Remainder	23	2.7905

result of extrusion or the development of a pressure wave. Damage to larvae at speeds in excess of about 8 m/second precluded our analysis of the ICWW data on a species basis. The high variability among blocks of trials would contribute to the variance around any regression equation used to adjust catches made at lower velocities.

Gear and Day-Night Comparisons

Numerous investigators (for example, Bowles and Merriner 1978), have recommended the need for gear-comparison studies to attain accurate quantitative estimates of larval-fish abundance. The results of our speed trials with the Miller high-speed sampler imply that quantitative surveys of larval fish larger than 10 mm may seriously underestimate true densities if gear is towed at less than 2 m/second, and that the gear employed should be calibrated for the effect of towing velocity. If gears are not calibrated, catch data may provide a distorted pic-

ture of the pattern of abundance and vertical distribution of some species. Recommendations regarding gear comparison and day-night sampling comparisons are particularly apt for situations in which most larvae are spawned offshore and move into estuarine nursery areas; older fish larvae are more capable of escaping slowly towed samplers than smaller oceanic-stage larvae (Aron and Collard 1969; Noble 1970; Colton et al. 1980). For many species, the ratio of night-to-day catches frequently increases with increased larval fish size. We therefore conducted one study to directly compare the Miller high-speed sampler and a 20-cm bongo net and a second study, with the Miller sampler only, to compare day and night catches.

Gear Comparisons

Significantly more Atlantic menhaden were collected at the water surface by the high-speed sampler towed at 5 m/second than by the 20cm bongo net towed at 2 m/second (Wilcoxon signed-ranked test; P < 0.01; Table 4). Although the ratio of the catch by the Miller net to that of the bongo net equalled or exceeded 3:1 for pinfish and Atlantic croaker at the surface, and for pinfish near the bottom, the variability was such that no significant differences were detected. Similarly, two-way chi square analyses (1 df) indicated that differences in catch of a species between the gears depended upon the depth of collection: Atlantic menhaden, $\chi^2 =$ 555, P < 0.001; pinfish, $\chi^2 = 6.40$, P < 0.02; Atlantic croaker, $\chi^2 = 3.98$, P < 0.05; spot, $\chi^2 =$ 3.37, P < 0.07.

Both visual avoidance of the approaching net by the larvae and their actual vertical distribution probably influenced the pattern of catches in these gear comparisons. Although only the Atlantic menhaden data conclusively show a

Table 4.—Mean daytime surface and bottom catches (±SE) of larvae in a 20-cm bongo net towed at 2 m/second and a Miller net towed at 5 m/second. The number of observations for each depth-gear combination was 10. Values are larvae/1,000 m³.

		Surface tows		Bottom tows		
Species	Bongo (B)	Miller (M)	M:B	Bongo (B)	Miller (M)	M:B
Atlantic menhaden	19 ± 5	198 ± 45	10.5	112 ± 59	173 ± 89	1.5
Pinfish	24 ± 9	108 ± 67	4.5	7 ± 6	21 ± 12	3.0
Spot	16 ± 10	23 ± 16	1.4	190 ± 67	351 ± 199	1.8
Atlantic croaker	1 ± 1	3 ± 1	3.0	14 ± 7	20 ± 8	1.4
Mean			4.9			1.9

Table 5.—Mean values for larvae collected on the surface and bottom during day and night. Values are larvae/1,000 m³ (±SE); the number of samples for each depth was 10. Samples were taken with the high-speed sampler towed at 5 m/second.

Species	Surface tows		Bottom tows	
	Day	Night	Day	Night
tlantic menhaden infish	420 ± 91 0	191 ± 43 18 ± 7	132 ± 109 1 ± 1	119 ± 26 6 ± 3
pot tlantic croaker	115 ± 65	797 ± 355 28 ± 11	60 ± 24 12 ± 5	0 ± 3 216 ± 50 39 ± 11

significant difference in catches by the two gears, the trends for all species suggested that visual cues and towing velocity are important in net avoidance. Both the Miller and bongo net data implied that pinfish were more concentrated near the surface (Table 4). In contrast, the observed patterns of vertical distribution for Atlantic menhaden were not consistent for the two sampling devices. The data for the Miller suggest a fairly uniform vertical distribution with a slightly higher density near the surface. Data for the more-slowly towed bongo net, however, implied that the density of this species was about six times greater near the bottom than near the surface, an observation which, when coupled with the high-speed data, suggest greater avoidance of the slower-moving bongo net at the surface.

The contrasting patterns of vertical distribution implied by the Miller and bongo-net samples raised questions that can be answered only with definite knowledge of the actual vertical distribution of the larvae. In the absence of this knowledge, we can only speculate about how much the difference in catches was due to light conditions favoring or restricting perception of approaching gears by larval fish. Because its catch per volume was consistently higher, we believe the Miller sampler provides a more accurate picture of vertical distribution than the slower 20-cm bongo net. We undertook a third study, with the Miller sampler alone, to clarify the vertical distribution patterns by comparing daytime and night catches.

Day-Night Comparisons

Among surface samples, night catches were significantly greater than day catches for pinfish, spot, and Atlantic croaker; Atlantic menhaden were more concentrated on the surface during the day (Tables 5 and 6). Our data on

Atlantic menhaden (19-26 mm) contrast with those of Kendall and Reintjes (1975), who often found no differences between day and night catches of smaller larvae (<10 mm) along the Atlantic Coast during 1965-1966; they towed a modified Gulf V net. To what extent these observations are due to visual avoidance or to changes in vertical distribution of a species is unknown. Differences we observed between surface and bottom catches of each species during the day were not apparent at night (Table 6), however, indicating either that there is a decrease in net avoidance during darkness or that distributions are more vertically uniform then. Our data thus support published suggestions that daylight sampling may underestimate larval densities for some species to a greater extent than night sampling.

Whereas 64% of the Atlantic menhaden collected in this phase of study were taken during the day, no more than 16% of the other species were (Fig. 2). Approximately 70% of all spots and pinfish were collected in surface waters

Table 6.—Computed levels of significance for Mann-Whitney U-tests for day-night catches of fish larvae. The four individual tests for a given species are not independent. Data are presented in Table 5.

	P level			
Species	Day versus night	Surface versus bottom		
Atlantic menhaden	Surface: <0.05 Bottom: <0.02	Day: <0.02 Night: NS		
Pinfish	Surface: <0.10 Bottom: NS	Day: NS Night: NS		
Spot	Surface: <0.10 Bottom: <0.02	Day: NS Night: NS		
Atlantic croaker	Surface: <0.02 Bottom: NS	Day: <0.05 Night: NS		

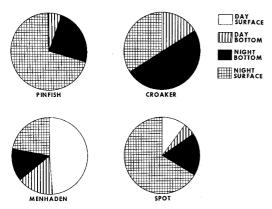


FIGURE 2.—Pie diagrams showing the proportions of pinfish, Atlantic croaker, Atlantic menhaden, and spot in the time-depth categories sampled near Beaufort, North Carolina.

during the night, whereas only 5 and 20% of the larvae of these species were collected near the bottom during day and night, respectively. On the other hand, 50% of the Atlantic menhaden were collected on the surface during the day; the same proportion of Atlantic croakers was collected at night near the bottom.

Data from daylight Miller high-speed sampling, both for gear comparisons (Table 4) and for day-night comparisons (Table 5), were consistent for Atlantic menhaden and Atlantic croaker. Atlantic menhaden were more abundant in surface than in bottom samples (sums, 618 and 305 larvae/1,000 m³, respectively). Use of 20-cm bongo-net tows alone, however, would have implied a much greater concentration near the bottom (Table 4). Atlantic croakers tended to be more abundant during the day in bottom than in surface samples (sums, 32 and 3 larvae/ 1,000 m³). Bongo-net samples also revealed this distributional trend (Table 4). The results for spot were not consistent for the Miller sampler during daylight; the gear-comparison study showed more larvae near the bottom but the day-night study showed more near the surface. The inconsistency is unexplained, but the summed values from these two phases suggest more spots near the bottom during daylight hours, as do bongo-net samples.

Conclusions

Net avoidance, among other factors, must be taken into consideration in larva-abundance studies. This point is particularly true in estuarine and nearshore habitats along the southeastern and southern coasts of the United States because larvae entering these nursery zones are larger than the smaller oceanic stages, and should have greater absolute burst speeds and avoidance potentials. Of the three types of studies we have presented, the speed-trial phase is the most easily interpreted because assumptions about vertical distribution of the larvae are not necessary. Our data showed that in the estuarine and nearshore areas we sampled, there was an increase in catch per unit volume as tow speed increased from 2 to about 8 m/second. The ICWW data indicated that losses of larvae possibly due to extrusion or to avoidance related to the development of a pressure wave in front of the net, were high at velocities above 8 m/second.

Our data from gear-comparison and daynight phases of the study were confounded by vertical distribution patterns of the larvae. Miller high-speed tows at 5 m/second provided estimates of average larva density that exceeded those of the 20-cm bongo net towed at 2 m/second by fivefold on the surface and twofold near the bottom. The differences between gears were most evident for Atlantic menhaden; the slower-moving bongo net showed maximum abundance of this species near the bottom, the Miller sampler near the surface. These comparisons show the need to calibrate gears for towing speed during studies of vertical distribution, because for one species, Atlantic menhaden, the pattern of vertical distribution implied by one gear was the reverse of that implied by the other. Atlantic menhaden appeared more concentrated in surface waters, particularly during the day, whereas the majority of spots and pinfish were collected in surface waters at night.

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